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Heterochrony, generic distinction and phylogeny in the family Hydractiniidae (Hydrozoa: Cnidaria)

F. Boero, J. Bouillon & S. Piraino

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F. Boero, Dipartimento di Biologia, Stazione di Biologia Marina, Università di Lecce, 73100 Lecce, Italy.
J. Bouillon, Laboratoire de Biologie Marine, Université Libre de Bruxelles, 50 Ave F.D. Roosevelt, 1050 Bruxelles, Belgium.
S. Piraino, Istituto Sperimentale Talassografico del CNR, Via Roma 3, 74100 Taranto, Italy.

Key words: Cnidaria; Hydrozoa; Anthomedusae; phylogeny; life cycle; classification; heterochrony; paedomorphosis.
The taxonomy of *Hydractinia, Stylactaria* and *Podocoryna* is discussed and the three genera are merged into *Hydractinia* since their diagnostic characters are liable to lead to polyphyly and paraphyly, due to repeated episodes of medusa reduction via heterochrony (paedomorphosis). The phylogeny of the Hydractiniidae is reconstructed by using two outgroups, *Clava* and *Cytaeis*, both having some characters in common with the Hydractiniidae. The resulting phylogenetic trees agree in identifying affinities among *Hydractinia, Kinetocodium* and *Hydrocorella*, all with polymorphic colonies with gastrozooids having oral tentacles. The position of *Clavactinia* (characterized by gastrozooids with widely scattered tentacles) is at the root of the tree if *Clava* is the outgroup, whereas it becomes apical when the outgroup is *Cytaeis*. The pattern of medusa suppression is different in the two cladograms, since the presence of a medusa is a plesiomorphic feature when *Cytaeis* is the outgroup, whereas it becomes apomorphic when the outgroup is *Clava*. These inconveniences are difficult to accommodate, since medusa suppression has occurred many times in the evolution of the hydroidomedusae, and Recent species do not witness past paedomorphic events of medusa reduction properly, so that many intermediate states are probably missing.

Introduction

Two genera of the family Hydractiniidae are widely used in experimental biology, namely *Hydractinia* and *Podocoryna*. A third allied genus, much less used for experimental research, is *Stylactaria*.

Previous studies of species of these genera have concentrated on regeneration (e. g., Achermann, 1980), embryology (e.g., Bodo & Bouillon, 1968; Kroiher & Plickert, 1992), myogenesis, gametogenesis and cnidogenesis (e.g., Boelsterli, 1977), induction of sexuality (e.g., Braverman, 1962), growth (e.g., Berrill, 1953; Braverman & Schrandt, 1969), tumor promotion (e.g., Kurtz & Schmid, 1991), expression of homeobox genes (e.g., Aerne et al., 1995, 1996), transdifferentiation (e.g., Schmid, 1988; Schmid et al., 1988; Reber-Müller et al., 1994), the organization of the extracellular matrix (e.g., Weber & Schmid, 1985; Reber-Müller et al., 1996), the coupling of ontogeny and phylogeny (e.g., Blackstone & Buss, 1992), the coupling of geological and molecular data in the reconstruction of symbiotic relationships (e.g., Cunningham et al., 1991), and paedomorphosis (e.g., Cunningham & Buss, 1993; Blackstone & Buss, 1993).

In spite of these contributions to experimental biology, and of being a classical

example of polymorphism in most textbooks on Cnidaria, the Hydractiniidae still do not have a settled generic taxonomy. Cunningham & Buss (1993) inferred relationships from molecular data of species of *Hydractinia, Podocoryna* and *Stylactaria* to test the phylogenetic meaning of medusa reduction in all hydroidomedusae. They showed that the three genera of the family are probably not monophyletic, an opinion shared also by Boero et al. (1996) from a preliminary comparative analysis of morphological characters. These findings support Petersen's (1990) criticism of the use of medusa suppression as a generic character.

Species, furthermore, are not easily identified and this is the first group of hydrozoans in which sibling species have been recognized (Buss and Yund, 1989), so that many experimental studies might have been made on material of dubious identity.

The characters used to distinguish *Hydractinia, Podocoryna* and *Stylactaria* will be reviewed to attempt a formalisation of shortcomings of current taxonomy, and to suggest evolutionary hypotheses that will be testable in future work with the aim of constructing a phylogenetic classification.

The morphological and phylogenetic basis for generic boundaries in *Hydractinia, Podocoryna* and *Stylactaria*

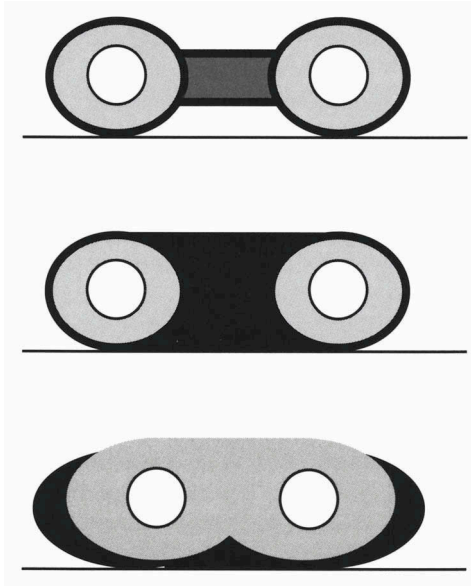
The genera *Hydractinia, Podocoryna* and *Stylactaria* are distinguished by the states of two main morphological characters:

1 - the structure of the hydrorhiza in fully grown colonies (fig. 1):
- reticular, formed by anastomosed stolons which remain separated (*Stylactaria* and some *Podocoryna*),
- encrusting, formed by anastomosed stolons covered by a common perisarc (some *Podocoryna*),
- encrusting, formed by anastomosed stolons covered by naked coenosarc after degeneration of the upper part of the stolonal perisarc sheath (*Hydractinia* and some species of *Podocoryna*).

2 - the structure of the gonosome:
- free medusae (*Podocoryna*).
- fixed or liberable eumedusoids (some species of *Hydractinia* and *Stylactaria*).
- fixed sporosacs (some species *Hydractinia* and *Stylactaria*).

The structure of the hydrorhiza, reticular or encrusting, has been generally accepted by recent authors as a generic character in the Hydractinoidea (Millard, 1975; Bouillon, 1985; 1995; Calder, 1988; Hirohito, 1988; Schuchert, 1996). This character, however, seems to depend sometimes on the nature of the substrate (see Edwards, 1972; Jarms, 1987; Hirohito, 1988). In many young or regenerating colonies of *Hydractinia* the hydrorhizae are reticulate but, nevertheless, the potential for the production of a layer of naked coenosarc is retained. For Blackstone & Buss (1991; 1992) reticulate forms are paedomorphic (progenetic) compared with encrusting ones. The growth of a hydractiniid colony, in fact, always starts with a reticulate hydrorhiza (thus, a juvenile character) which then becomes encrusting by anastomosing.

According to 'classic' views on hydroidomedusan phylogenetic characters (reviewed by Cunningham & Buss, 1993), the presence of free medusae is a plesiomorphic feature, whereas medusa reduction represents a derived state. In this framework, *Podoco-*



Podocoryna - Stylactaria
non-encrusting, reticular hydrorhiza formed by anastomosing stolonal tubes surrounded by perisarc

Podocoryna
encrusting hydrorhiza formed by coalescent stolons leading to a perisarc-covered mat

Podocoryna - Hydractinia
encrusting hydrorhiza formed by coalescent stolons whose perisarc degenerates in the upper portion leading to a coenosarc-covered mat

Fig. 1. Schematic representation (in section) of hydrorhizal features of the three main genera of the Hydractiniidae. Black: perisarc; dark grey: surface of transverse hydrorhizal tube connecting two main hydrorhizal tubes; light grey: coenosarc.

ryna should have plesiomorphic features linked to the presence of free medusae and, also, to the possession of hydrorhizal character states covering all the possibilities listed above, being either reticular, perisarc- or coenosarc-covered mat-like. *Stylactaria* should represent a monophyletic clade with medusae reduced to eumedusoids, and a reticular hydrorhiza (both features as a result of paedomorphosis). *Hydractinia* should be a monophyletic clade with medusae reduced to paedomorphic eumedusoids or to sporosacs, and with stolonal differentiation into an elaborated mat of coenosarc, a plesiomorphic feature present also in some *Podocoryna*.

The morphological overlaps in generic characters among the three taxa, along with the incongruences stressed by Cunningham & Buss (1993) using molecular data, call for reconsideration of the value given to generic characters in reconstructing phylogenies.

Sibling species and sibling genera, or: are ancestors real?

Assignment of species to separate genera on the basis of differing medusa expression (due to paedomorphosis) has been criticised by Petersen (1979; 1990), since paedomorphic patterns have been shown in a few genera to have arisen more than once. This view has been supported within the Hydractiniidae by molecular evidence provided by Cunningham & Buss (1993). The same argument might be used for the type

of hydrorhizal organisation, so that colonies with paedomorphic features (such as those assigned to *Stylactaria*) might be the result of independent phenomena of heterochrony affecting the expression of both medusa and hydrorhiza.

It might be possible that a paedomorphic species deriving from a *Podocoryna*-like ancestor originated a monophyletic clade which could be recognised as a sound genus. But paedomorphic species deriving from other *Podocoryna*-like ancestors might evolve the same morphology independently, so that one could consider them as belonging to 'sibling genera' (fig. 2).

Under such circumstances, the monophyletic clade might still be considered as a genus, but the isolated paedomorphs should remain connected to the 'ancestral' genus. Petersen (1979, 1990) argued that in a few genera medusa loss has probably occurred more than once within the same clade, thus leading to polyphyletic taxa as based on a generic character not correlated with other autapomorphies. For this reason the paedomorphs are to be assigned to the same genus of the non-paedomorphic species, if no other characters diverge from the ancestral state. However, if, as suggested above, an event of medusa reduction were followed by radiation of species retaining that character, the result might be a monophyletic clade of possible generic rank.

In all evolutionary studies based on living species, it is almost impossible to recognise sister species from 'mother' species. Cladism, furthermore, considers ancestors as idealised entities with plesiomorphic features, whereas it is undeniable that ancestors are not ideas but species, at least as much as their descendants (Rasnitsyn, 1996). It is not inconceivable that a still living species originated a group of species by cladogenesis, while remaining unmodified or going through anagenesis in its core population(s). These events, in both morphological and molecular studies, might lead to identification of 'sisterhood' and not of 'motherhood'. Palaeontology might help in solving the problem, but the fossil record of hydractiniids is too scarce to be of use.

The lack of consistency found by Cunningham & Buss (1993) while comparing genome fractions of *Hydractinia, Podocoryna* and *Stylactaria* might suggest that single species assigned either to *Stylactaria* and *Hydractinia* originated independently from *Podocoryna*-like ancestors, leading to polyphyletic (*Stylactaria* and *Hydractinia*) and paraphyletic (*Podocoryna*) taxa, as suggested by Boero et al. (1996) (fig. 2).

Being 'plesiomorphic', the *Podocoryna* set of characters might lead to grouping species into a compact clade, also from a molecular point of view. The compactness of the clade, however, should not be necessarily an indication of monophyly, but only of lack of deviation from an ancestral state.

The cladogram proposed in fig. 2 is rather unorthodox, since it represents ancestors as real taxa. Furthermore, it is characterised by several parallel events of evolutionary change. However, if a change is due to addition of new characters (e.g., the acquisition of a medusa stage), it is unparsimonious to propose independent origins of the same character, but if the change is due character simplification (e.g., the loss of a medusa stage via paedomorphosis), the possibility of parallel events is not to be considered as unparsimonious as in the former case. Medusa suppression has occurred in the Hydroidomedusae independently so many times (see Bouillon, 1985; Petersen, 1990; Cornelius, 1992) that is currently considered as a very probable event.

Currently, the only way to avoid the unnatural taxa deriving from the situation

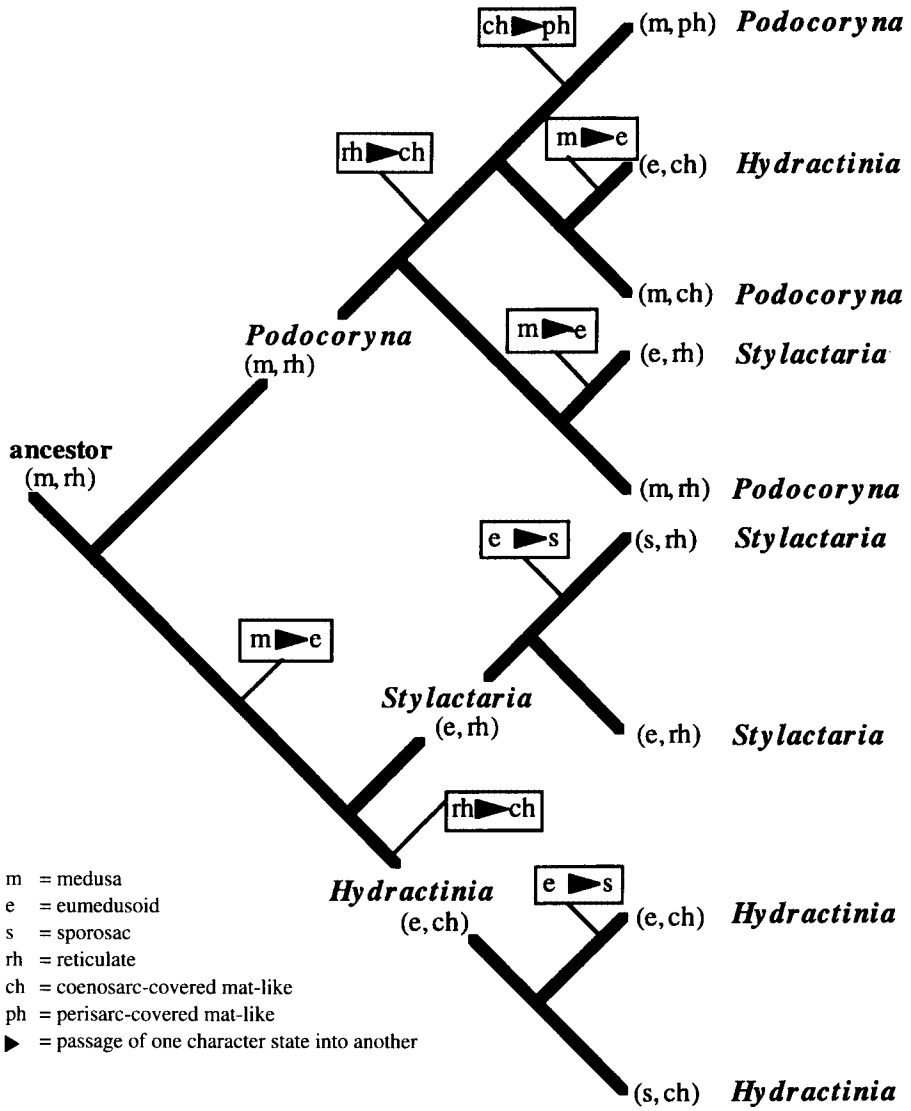


Fig. 2. Hypothetical phylogenetic scenario showing the possibility of the polyphyly of the currently recognised hydractiniid genera with reduced medusae (*Stylactaria* and *Hydractinia*), and of the paraphyly of the genus comprising species with medusae (*Podocoryne*).

depicted in fig. 2 is to merge both polyphyletic and paraphyletic genera, so as to have a monophyletic clade, even if of very remote ancestry. So we propose here to merge the main three genera of hydractiniids (*Hydractinia* van Beneden, 1841; *Podocoryna* Sars, 1846; *Stylactaria* Stechow, 1921) into the oldest one: *Hydractinia* van Beneden, 1841. Similar positions have been taken already by several authors: Motz-Kossowska (1905) merged *Hydractinia, Podocoryna* and *Stylactaria* (= *Stylactis*) into *Hydractinia;*

Broch (1914) considered that *Stylactaria* and *Hydractinia* could not be kept apart; and Naumov (1960/1969) merged *Podocoryna* into *Hydractinia*. Kramp (1932) gave *Podocoryna* and *Stylactaria* subgeneric rank within *Hydractinia*, but this is not phylogenetically sound. If *Podocoryna* and *Stylactaria* were monophyletic, they could well be ranked as genera; if they are not monophyletic (as it is suggested here), they are unsound even as subgenera.

These inconveniences cannot be avoided in morphological studies; molecular approaches might help in distinction of monophyletic clades from 'sister clades' sharing medusa reduction, thus identifying what could be possibly called 'sibling genera'.

The diagnosis of *Hydractinia* van Beneden, 1841

Colonies with a stolonal reticular hydrorhiza formed by tubes covered with perisarc, or with an encrusting hydrorhiza covered with perisarc or with naked coenosarc; typically with simple, canaliculated or branched spines. Hydranths sessile, naked, polymorphic: gastrozooids, gonozooids, and occasionally dactylozooids. Gastrozooids with one or more close whorls of tentacles encircling the hypostome; gonozooids with one or more close whorls of tentacles, or without tentacles and/or hypostome, being reduced to blastostyles; dactylozooids without tentacles. Gonophores: either fixed sporosacs, liberable or retained eumedusoids, or free medusae, arising from varyingly developed gonozooids or directly from the hydrorhiza. Medusae more or less bell-shaped. Four radial canals; four or more solid and simple marginal tentacles, with or without ocelli. Manubrium with or without peduncle, tubular or sac-shaped, with four or eight simple or slightly branched oral arms (dilatations of the mouth rim) armed with clusters of cnidocysts. Gonads on manubrium, generally interradial but sometimes extending to the proximal portion of radial canals. Sometimes asexual reproduction by medusa budding on manubrium.

The phylogeny of the Hydractiniidae

Bouillon (1995) assigned the following living genera to the Hydractiniidae: *Clavactinia* Thornely, 1904; *Hansiella* Bouillon, 1980; *Hydractinia* van Beneden, 1841; *Hydrocorella* Stechow, 1921; *Janaria* Stechow, 1921; *Kinetocodium* Kramp, 1921; *Podocoryna* Sars, 1846; *Stylactaria* Stechow, 1921; and *Tregoubovia* Picard, 1958. Bouillon (1985; 1995) also listed a series of fossil genera doubtfully assigned to this family because of skeletal remains, but the paucity of diagnostic features makes them useless for a phylogenetic reconstruction of the family and they will not be considered here.

Both *Hansiella* and *Tregoubovia* are medusa-based genera, their hydroids being unknown. The medusa of *Thecocodium quadratum* (Werner, 1965) (family Ptilocodiidae) described by Jarms (1987), however, shares some key features with the medusae of the two above mentioned genera, namely a marginal nematocyst ring and didermic exumbrellar processes, and this will allow assignment of both *Hansiella* and *Tregoubovia* to the Ptilocodiidae (Bouillon et al., 1997). *Hydractinia, Podocoryna* and *Stylactaria* are here merged into *Hydractinia* (see above). *Hydrocorella* and *Janaria* are characterized by a calcareous skeleton. Generic differences are minor for the purpose of this revision and the two genera will be treated together under *Hydrocorella* even if they

are to be considered as separate (see Cairns & Barnard, 1984 for a treatment of *Janaria*). *Kinetocodium* comprises only one species which has been found a few times, epizoic on pteropods (Kramp, 1921; 1957). Only the young medusa is known and its position is still uncertain, pending knowledge of its complete life cycle. Thus, for ease of analysis, the Hydractiniidae is considered here to comprise *Clavactinia, Hydractinia, Kinetocodium* and *Hydrocorella.*

The outgroups of the Hydractiniidae

The key features of the Hydractiniidae (see above for details) are the presence of naked hydranths deprived of stem, directly connected to a hydrorhizal system which can be a more or less elaborated network. The hydranths are polymorphic, being distinguished in tentacled gastrozooids, and gonozooids. In many species both dactylozooids and spines are present. The medusae, when present, have oral lips armed with nematocysts which can be arranged in clusters (*Podocoryna*) or in a single continuous row (*Kinetocodium*).

A survey of all other Anthomedusae (from Bouillon, 1985) for the choice of an outgroup indicates two genera as best candidates:

- *Clava* (family Clavidae) shares with the Hydractiniidae the presence of naked hydranths deprived of stem, directly connected to a hydrorhizal system which can range from simple stolons to a network of tightly anastomosed stolons sometimes becoming covered, as reported by Hincks (1868) and Motz-Kossowska (1905), by a layer of perisarc. Contrary to the Hydractiniidae, *Clava* is monomorphic and its gonophores, as fixed sporosacs, originate on undifferentiated hydranths. Fraser (1946: 138) considered that *Stylactaria* "must have come directly from the Clavidae".
- *Cytaeis* (family Cytaeidae) shares with the Hydractiniidae the presence of naked hydranths deprived of stem, directly connected to a reticular hydrorhiza, but is monomorphic, and the gonophores arise from the hydrorhiza. The medusae have oral tentacles inserted above the mouth.

The polarisation of the Hydractiniidae

Clava as an outgroup.— The hydractiniid genus with characters closest to *Clava* is *Clavactinia.* In both genera the hydranths are naked and have scattered tentacles, but *Clavactinia* is polymorphic and its hydrorhiza is covered by naked coenosarc (see Millard & Bouillon, 1973 for a detailed description). Both genera lack a medusa stage. All the other genera of the Hydractiniidae have tentacles concentrated around the mouth, in one or multiple but closely set whorls (for this reason we include *Clavactinia multitentaculata* Millard, 1975, in *Hydractinia*). *Hydractinia,* widely discussed above, is characterised by polymorphism, gastrozooids with oral tentacles, and by the presence of medusae with oral lips armed with nematocyst clusters. *Kinetocodium* is kept separate from *Hydractinia* because gonozooids are absent, and its medusae originate directly from the hydrorhiza and have a continuous ring of nematocysts around the mouth, instead of nematocyst clusters. *Hydrocorella* has polymorphic colonies with fixed gonophores and is separated because its hydrorhiza is calcareous, resembling that of

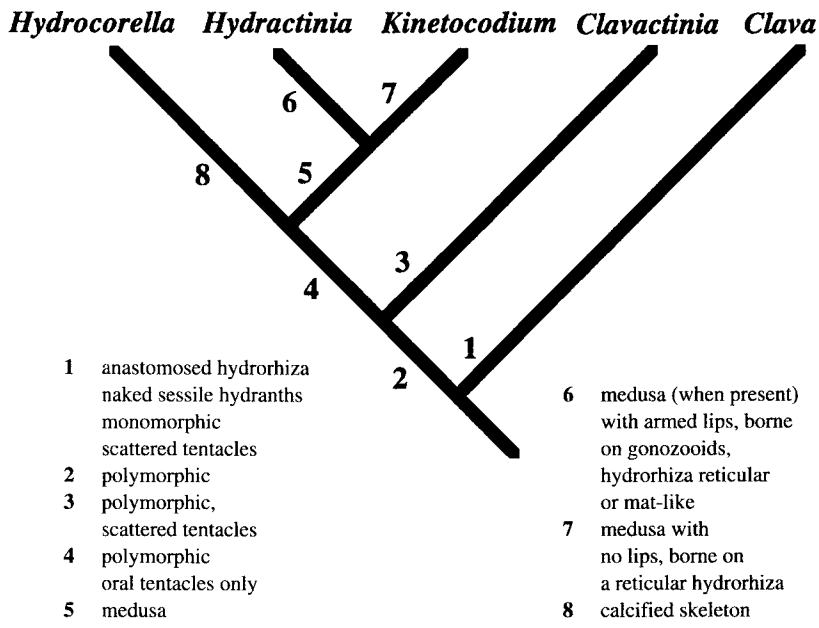


Fig. 3. Cladogram of the Hydractiniidae with *Clava* as an outgroup.

a hard coral. The resulting cladogram is presented in fig. 3.

Cytaeis as an outgroup.— Both *Cytaeis* and some species of *Hydractinia* (those formerly assigned to *Podocoryna*) share the presence of a medusa. The main difference is that in *Cytaeis* the oral zone of the manubrium is armed with oral tentacles inserted above the mouth, whereas in *Hydractinia* the mouth is armed with more or less developed nematocyst clusters borne directly on the lips. Besides this feature, the medusae of the two families are quite similar. The hydrorhiza of *Cytaeis* is reticular, as is that of some species of *Hydractinia.* The hydranths, furthermore, are similar, even though *Cytaeis* is monomorphic. As in the cladogram resulting from the choice of *Clava* as an outgroup (fig. 3), the genera *Kinetocodium* and *Hydrocorella* are close to *Hydractinia,* whereas *Clavactinia* is separated from the rest of the clade by the presence of scattered tentacles. The resulting cladogram is given in fig. 4.

The comparison of the cladograms deriving from the two chosen outgroups (figs. 3 and 4) show that when *Clava* is the outgroup, *Clavactinia* has plesiomorphic features, whereas its scattered tentacles become apomorphic if *Cytaeis* is the outgroup. The presence of a medusa stage, when *Clava* is the outgroup, is not connected with ancestral features, and this leads to the hypothesis that ancestral species with medusae and widely scattered tentacles became extinct or are still to be discovered. The hypothesis is supported by the presence of two genera with medusae (*Turritopsis* and *Oceania*) in the Clavidae. Their hydroids have erect, branched stems, being noticeably different from those of the Hydractiniidae, but their medusae are very similar to those of the Hydractiniidae, and there might be no justification for keeping them in separate families, if their hydroids were not so different.

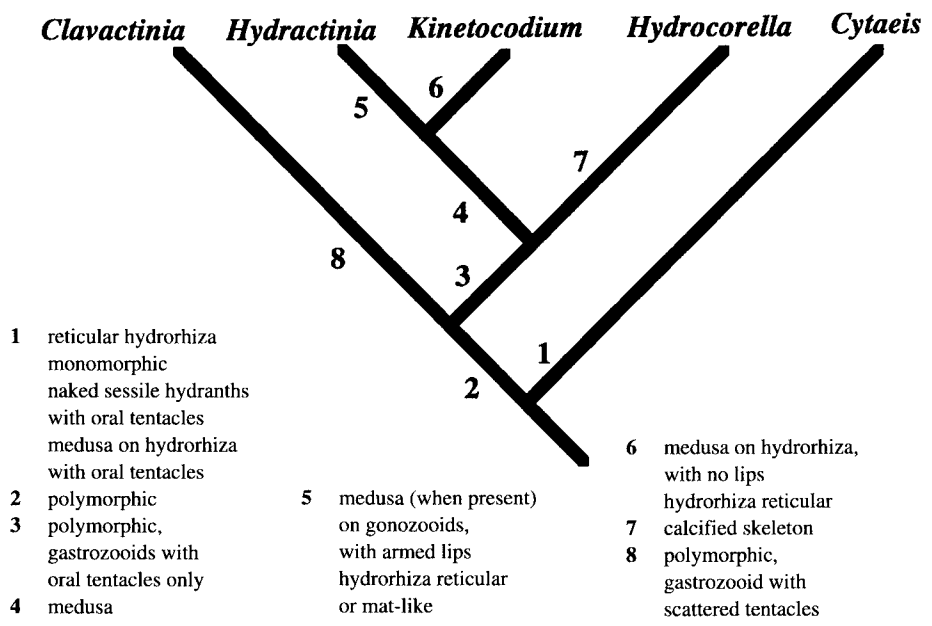


Fig. 4. Cladogram of the Hydractiniidae with *Cytaeis* as an outgroup.

When *Cytaeis* is the outgroup, there is no need for the extinction of ancestors with medusae, since both *Cytaeis* and some *Hydractinia* have medusae and naked feeding hydranths with a single row of tentacles, originating from a reticular hydrorhiza. The main difference in the medusae of *Cytaeis* and *Hydractinia* is the presence of oral tentacles in the former. The passage from *Cytaeis* to *Hydractinia* leads one to hypothesise the loss of the oral tentacles (reduced to nematocyst clusters) and the evolution of polymorphism.

Conclusion

The scope of *Hydractinia* still remains doubtful, due to lack of information about the genera here merged with it: *Podocoryna* and *Stylactaria*. It might be possible that monophyletic clades of species falling within the scope of *Hydractinia* and *Stylactaria* really exist, but that repeated heterochronic events in *Podocoryna*-like ancestors led to 'sibling genera'. The Hydractiniidae have strict affinities with both the Clavidae and the Cytaeidae.

The problem of medusa loss raises some problems in phylogenetic analysis. It is conceivable, that all families with medusae originated from ancestors with medusae, and that medusae were lost independently in the various families. The hypothesis that such elaborate morphs as the medusae evolved independently in many clades with no medusa requires far too unlikely parallel events. Some families, furthermore, have no species with medusae. Medusa reduction or loss by paedomorphosis has occurred repeatedly and independently during hydroidomedusan evolution resulting

in similarity in morphology perhaps being unreliable as a point of reference in some genera. The grouping of all species with reduced medusae in clades separate from those of similar species with medusae, in fact, is more parsimonious than considering them as originated by possible parallel events, but this is the case in a few known examples (as convincingly argued by Petersen, 1990), in spite of being less parsimonious.

Comparison of the two cladograms derived using different outgroups (figs 3 and 4), in this framework, makes *Cytaeis* a better outgroup than *Clava*, because in this case both the outgroup and the stem species of the family have the plesiomorphic feature of a medusa stage. When *Clava* is the outgroup, the medusa appears as a newly-acquired feature, a less parsimonious conclusion, as hypothesized above (but medusae could become suppressed in some clades while having the possibility of being re-expressed in the course of evolution, as argued by Boero et al., 1996). *Clava*, furthermore, is referred to the distant family Clavidae solely on the basis of its scattered tentacles, but such a feature is proving to be shared by many species referred to different families and is possibly not a good family character. The hydrorhizal system of *Clava* closely resembles that of some *Hydractinia* species and future molecular studies will possibly better define the affinities of these taxa and the whole phylogeny of the Hydractinidae.

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This paper is dedicated to our friend and colleague Wim Vervoort, whose work on hydrozoans will remain an invaluable exploration of the diversity of the group.

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